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Comment

Granularity of the mirror neuron system: A complex endeavor Comment on "Grasping synergies: A motor-control approach to the mirror neuron mechanism" by A. D'Ausilio et al.

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The review paper by D'Ausilio and coauthors [3] is very timely and addresses one of the long-standing issues with respect to the coding features of mirror neurons. Through the history of mirror neuron research, there has been some controversy with respect to the level of granularity of the mirror neuron system, as studied in animal and human systems. While some researchers have suggested that abstract (high level) features of movement are coded, others have claimed evidence for more muscle specific (low level) coding properties (for an example, see [1,2]). D'Ausilio et al. [3] take a strong position in their review, suggesting a convergence between basic mechanisms of movement control and the mirror neuron system. Their suggestion is inspired by Bernstein's influential work on the so-called degrees of freedom problem. Even though a goal can in principle be reached in an infinite number of ways, consistent and stereotypical patterns of kinematics and muscle activation are often observed [4]. This has led to the notion of movement synergies as the basic building blocks for movement control. Even though it is essentially possible to contract isolated muscles or even motor units, Bernstein suggested that control of complex movement relies on movement synergies or coordinative structures, referring to a group of muscles that behave as a functional unit. This reduces the computational demands of the central nervous system considerably by assigning more responsibility to the lower levels of the movement control system. Bernstein's approach has inspired the dynamical systems perspective that has focused on a better understanding of complex biological systems such as interlimb coordination in humans [8]. For example, the upper limbs behave as a coordinative structure whereby simultaneous activation of the homologous muscle groups constitutes the default or preferred coordination mode that has to be defied when alternative patterns of coordination need to be performed or learned [8,10]. Additional support for such larger building blocks or basic postures in the upper limbs has also been provided by electrical stimulation of motor cortical areas in nonhuman primates [6]. The important inference made by D'Ausilio et al. [3] is that research inspired by the mirror neuron system, such as noninvasive brain stimulation using TMS, should go beyond the registration of motor evoked potentials in single muscles and instead monitor activity in multiple muscles to reveal the operation of these motor synergies. We

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fully agree that this is an important methodological recommendation for future work because previous TMS research paradigms may have constrained our view on granularity of the mirror neuron system.

Whereas we are sympathetic towards the authors' perspective on the granularity of the mirror neuron system, we suggest it should be embedded within a broader perspective on neural representations of movement. This concept is consistent with a hierarchical control perspective in which an abstract movement goal or intent is transformed into a concrete movement plan that finally evolves into the recruitment of appropriate muscle synergies. The notion of hierarchical control was already implicitly evident in Liepmann's [9] seminal work on apraxia patients in which high level features of movement are primarily considered to be represented in left parietal cortex from where this information is made accessible to left and right (pre)motor structures to gradually specify the details of movement. In other words, Liepmann considered the left parietal cortex as a critical neural site for motor engrams or skilled motor representations. Consequently, movements made by either the left or right side of the body (or both) will give rise to more overlap in activation in the parieto-frontal areas of the left hemisphere and these areas are candidates for more abstract (effector-independent) representations [11]. Therefore, the left parieto-premotor complex, more so than the right, represents the neural correlate of motor equivalence, a hallmark of central nervous system flexibility in reaching action goals through various means. Accordingly, the question about the coding of high versus low features of movement may extend beyond the mirror neuron system and should be answered in view of hemispheric specialization within the larger set of brain areas constituting the action control network that entails different levels of movement coding. Such a hierarchical perspective gives way to different levels of motor encoding specificity as the final stages of motor command generation in the motor cortical areas are approached. The question then emerges where exactly in the movement control hierarchy mirror neurons are present. It is conceivable that mirror neurons may exhibit a different level of granularity depending on where in the brain they reside, which in itself is an ongoing matter of intense debate.

Another important message underlined by D'Ausilio et al. [3] refers to the link between level of skill or expertise and granularity of the mirror neuron system. This argues for a dynamic perspective on encoding in neurons, including mirror neurons. More skilled performers are not only more successful command generators but have also developed more refined representations of sensory consequences associated with correct movement. In other words, experts are also more sophisticated observers [5]. Their action observation network is gradually tuned to the specific sensory information associated with successful action, resulting in better prediction of their own and others actions. Such a dynamic view on granularity of action coding implies an evolution from general to more specific encoding of movement and its sensory consequences.

Our final comment refers to a potentially meaningful paradigm that may provide a critical test for D'Ausilio et al.'s perspective on the mirror neuron system. Even though the mirror neuron concept has inspired a considerable amount of research on single limb reaching/grasping, it is somewhat surprising that so little research has been done on bimanual movements even though these are abundant in everyday life, e.g., opening a bottle, peeling a banana, tying shoelaces etc. Bimanual skills may constitute a critical testing ground for the authors' viewpoint on mirror mechanism granularity because the abstract movement goal (successfully opening the jar of a bottle) emerges from differential contributions of each hand. Whereas the dominant hand is typically involved in performing the focal action (turning the jar), the nondominant hand serves to stabilize the object (holding the bottle and counteracting the forces generated by the dominant hand), providing the background against which the focal action can be produced. As such, the individual limbs generate distinct kinematics and patterns of muscle activation, giving rise to the abstract unified movement gestalt or intended goal (opening the bottle). The question is whether, how and where the low and high level coding of bimanual movement is accomplished within the distributed brain network that spans across both hemispheres. From an action observation perspective, fMRI work suggests that observation of unimanual and bimanual movements activates a similar occipito-temporo-parieto-premotor network even though nodes of this network function differently under bimanual and unimanual action observation conditions [7].

In summary, the exploration of mirror neuron granularity will be an exciting but also very challenging endeavor because it may be dependent on brain locus, expertise level, task, and experimental context.

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